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Review

The late Quaternary crocodylian record from Australasia

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ABSTRACT

In this study, we synthesize the known late Quaternary crocodylian record in Australasia through literature review and direct assessment of fossil and zooarchaeological material. The late Pleistocene record, mainly from Australia, consists of partial skeletal remains mostly referable to the extinct Mekosuchinae, with some attributable to *Crocodylus*. The youngest reliably dated mekosuchine fossil is ~20000 years old, suggesting mekosuchine decline and extinction coincided with that of other Australian megafauna. In contrast, three south-west Pacific islands—New Caledonia, Vanuatu, and Fiji—were Holocene refuges for mekosuchines, whose remains occur in archaeological contexts, indicating human interaction. Their extinction followed soon after human arrival, suggesting anthropogenic influence as a potential key factor. *Crocodylus johnstoni* occurs in palaeontological (potentially 28 kya) and archaeological sites in Australia. *Crocodylus porosus* has an ambiguous fossil record potentially going back over 40 kya, but is definitively present by the Holocene. Most *Crocodylus* remains come from coastal sites overlapping modern ranges. Archaeological evidence supports crocodile utilization by humans in Australia, Torres Strait, and New Guinea. The fragmentary nature of the known fossil material, as well as the current lack of reliable dates, leaves many unanswered questions about the morphology, palaeobiology, and disappearance of mekosuchines.

Keywords: crocodile; Mekosuchinae; Oceania; Pleistocene; Holocene; extinctions

INTRODUCTION

Crocodylia Gmelin, 1789 is a remarkable clade of archosaurian reptiles that has a long evolutionary history spanning from the Cretaceous to the present (Brochu 2003, Grigg and Kirshner 2015, Rio and Mannion 2021). Today, there are nine extant crocodylian genera containing 27 to 28 recognized species, with some of them being species complexes that encompass two or more distinct taxa that are yet to be formally named (e.g. Grigg and Kirshner 2015, Bittencourt *et al.* 2019, Brochu and Sumrall 2020, Avila-Cervantes *et al.* 2025). Extant crocodylians have a broad distribution across tropical and subtropical biomes where they play vital roles in their environments, typically as apex predators and ecosystem engineers. As carnivorous animals capable of preying on hominins, large crocodylians were important predators during key stages of human evolution (Brochu *et al.* 2010, Brochu and Storrs 2012, Njau and Blumenschine 2012). Historically, in regions where the ranges of crocodylians and humans have overlapped, their interactions have influenced human cultural

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traditions and spiritual beliefs (e.g. Dinerman 1981, Telban 2008, Zecchi 2010, Anwana *et al.* 2012, Fijn 2013, Gonzales *et al.* 2013, Pooley 2016, Tsuji 2021, Akhmar *et al.* 2023). For example, in the islands of Timor and Wetar to Australia's north, the Indo-Pacific (or saltwater, estuarine) crocodile (*Crocodylus porosus* Schneider, 1801) is widely regarded as a sacred animal and an ancestor (Brackhane *et al.* 2019, S. O'Connor pers. obs. 2024). It is central to the creation myth of the island of Timor whose shape is said to resemble a half-submerged crocodile 'with its head to the east and tail to the west' (McWilliam 2007: 366). In Timor-Leste crocodiles are called 'grandfather' and revered, and this status means they are rarely killed (Brackhane *et al.* 2019). Conversely, in other parts of the world where humans and crocodylians overlapped, interactions with humans have resulted in the significant decline of crocodylian populations or even their extinction (e.g. Iijima *et al.* 2022).

In Australasia (a subregion of Oceania incorporating Australia, Aotearoa New Zealand, New Guinea and surrounding islands, and Melanesia), crocodylians have been part of faunal communities for tens of millions of years, particularly in mainland Australia. This is still the case, although their taxonomic diversity has declined significantly since the late Pleistocene, with only four species of *Crocodylus* Laurenti, 1768 still extant. Present-day Australasia is inhabited by three endemic species of *Crocodylus: C. novaeguineae* (Schmidt, 1928) and *C. halli* Murray *et al.*, 2019 in New Guinea, and *C. johnstoni* (Krefft, 1873) in Australia. [Note that Agne *et al.* (2026) did not find support for *C. halli* as a distinct species from *C. novaeguineae* based on mitochondrial data.] The fourth, *C. porosus*, is the largest living reptile and inhabits a vast range from south and south-east Asia into northern Australasia (New Guinea and surrounding islands, the Torres Strait, and northern parts of Australia), and Melanesia (Webb *et al.* 2021). Based on the known fossil record, species of *Crocodylus* have been present in Australia and New Guinea since the Pliocene, although their taxonomy is yet to be fully resolved as they include currently unnamed and undescribed extinct species of the genus (Molnar 1979, Yates and Pledge 2017, Yates 2019, Ristevski *et al.* 2023a, 2025).

The most species-rich crocodylians from the Cenozoic of Australasia were the now extinct members of Mekosuchinae Willis *et al.*, 1993. Mekosuchine crocodylians were a diverse group that included species with disparate craniomandibular morphologies, body sizes, dental types, and distinct palaeoecologies (e.g. Molnar 1982a, Megirian 1994, Willis 1993, 1997a, b, 2001, 2006, Salisbury and Willis 1996, Buchanan 2009, Stein *et al.* 2012, 2015, 2017, 2020, Yates 2017, Yates and Pledge 2017, Ristevski *et al.* 2020, 2023b, Ristevski 2022, Yates *et al.* 2023, Yates and Stein 2024; for a recent exhaustive review, see: Ristevski *et al.* 2023a). Outside of Australia, mekosuchines are also known from several islands in the south-west Pacific and some New Guinean crocodylian fossils are almost certainly mekosuchine as well (Ristevski *et al.* 2025).

Crocodylians inhabited Sahul (the combined landmass of present-day Australia, Lutruwita/Tasmania, Torres Strait islands, and New Guinea and some surrounding islands due to lowered sea levels) long before the first humans arrived on the continent and would have been part of the fauna that humans encountered when they first settled the region. Extant species of *Crocodylus* are significant to many Indigenous cultures and language groups across northern Australia, the Torres Strait, and New Guinea, and, like many other animals, are sometimes hunted for food, artefact manufacture, and other purposes (e.g. Trezise 1977, Wright 2011, Fijn 2013, Akerman 2018, Telban 2018; read below). Given the continuing ecological and cultural significance of crocodylians in Australasia, their evolutionary history and taxonomic diversity provide important context for understanding both past ecosystems and contemporary human–crocodylian relations and interactions, as well as late Quaternary megafauna extinctions.

Recently, a comprehensive review of crocodyliform evolutionary history in Australasia was published by Ristevski *et al.* (2023a), covering the fossil record from the Early Cretaceous to the Holocene, as understood at the time of that writing. Ristevski *et al.* (2023a) also reviewed the late Quaternary record from the south-west Pacific and mainland Australia; however, the focus of that study was not on the zooarchaeological record from the region. Here, we provide a synthesis of all currently known Australasian crocodylian material from the late Quaternary, drawing on a review of the published literature, as well as first-hand assessment of relevant palaeontological and zooarchaeological material to assess the nature and timing of human–crocodylian interactions in the region. This synthesis also examines the potential application of archaeological and palaeoecological data to understanding long-term ecosystem dynamics in Australia, as well as the conservation of crocodylians in the Anthropocene (Boivin and Crowther 2021, Boivin *et al.* 2024). A comprehensive review identified 26 fossil and archaeological sites from the late Quaternary of Australasia that have produced crocodylian remains (Fig. 1), and their contents are summarized below.

Importantly, this study does not draw on the knowledge on crocodylians that is part of many diverse cultures across the ranges where crocodylians occur or have occurred, as it is beyond the scope of this paper. For these reasons, we have restricted our commentary on rock art and associated cultural knowledge systems and how these have been interpreted to that which has been published previously in the archaeological and anthropological literature.

Institutional abbreviations mentioned in the text

AM, Australian Museum, Sydney, New South Wales, Australia; CPC, Commonwealth Palaeontological Collections, Canberra, Australian Capital Territory, Australia; NCP, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, London, England, UK (OR, old register); NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, Aotearoa New Zealand; QM, Queensland Museum, Brisbane, Queensland, Australia; UF, University of Florida Museum of Natural History, Gainesville, Florida, USA.

SYNTHESIS OF THE LATE QUATERNARY CROCODYLIAN RECORD FROM AUSTRALASIA

The late Quaternary record of mekosuchine crocodylians

Mainland Australia

An important preamble on the late Pleistocene mekosuchine record from mainland Australia is that, at the time of this writing, only one specimen (QMF59869) has had its minimum age estimated through uranium-series (U-Th) dating [see

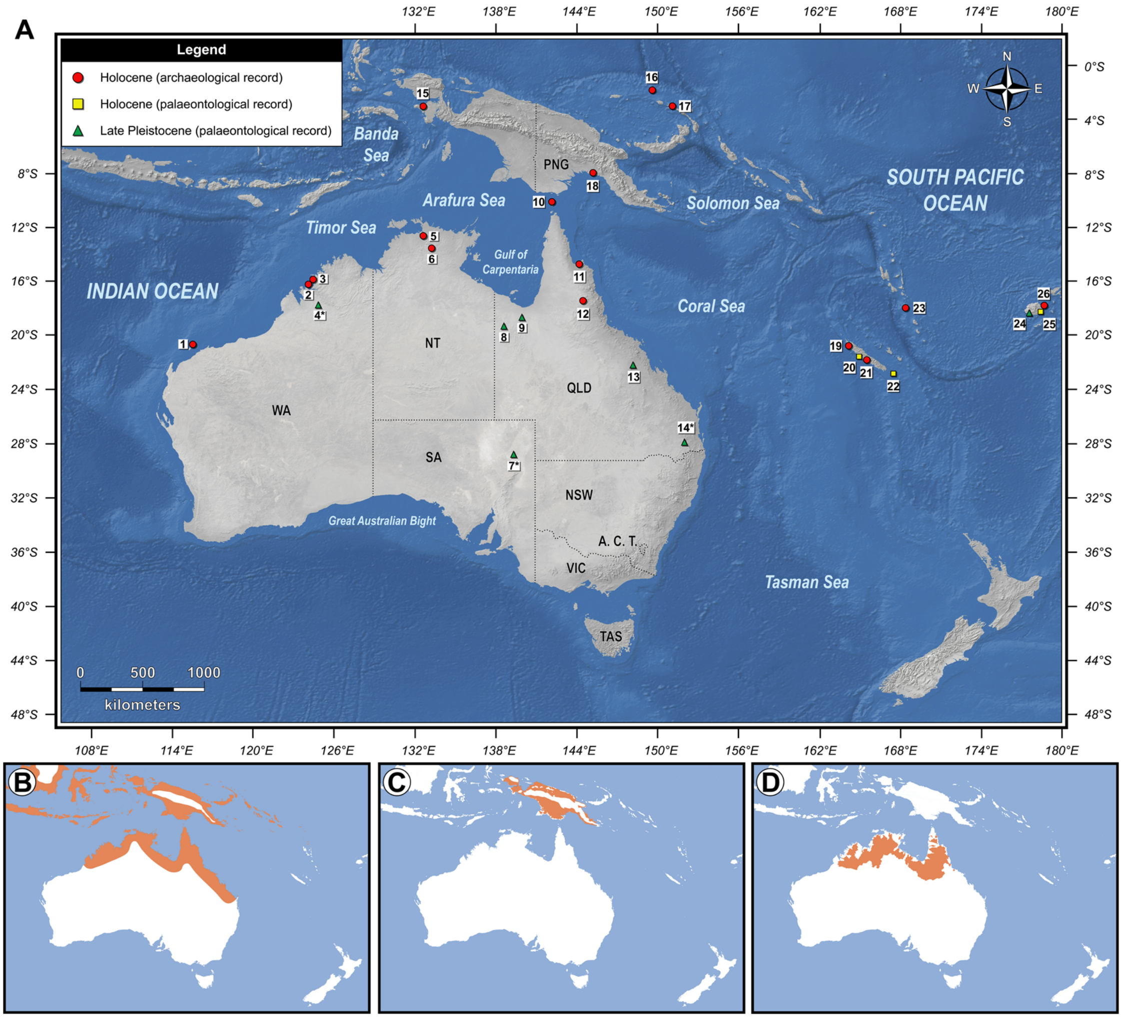

Figure 1. Late Quaternary crocodylian distributions in Australasia. A, relevant palaeontological and archaeological localities across Australasia that have yielded crocodylian remains (as known at the time of this publication). Only sites that have been reported as late Pleistocene and Holocene are indicated, whereas sites that are middle and early Pleistocene, or sites of uncertain Pleistocene age are not shown. Material that is tentatively assigned to the late Pleistocene is indicated with an asterisk. For a complete map of all Pleistocene localities (as well as all other known Cenozoic and Mesozoic sites), see figure 2 of Ristevski *et al.* (2023a). B, approximate modern distribution of *Crocodylus porosus* in Australasia [based on Grigg and Kirshner (2015) and Webb *et al.* (2018); note that distributions further north-west into south and south-east Asia are not shown]. C, approximate modern distribution of *Crocodylus novaeguineae* [based on Solmu and Manolis (2019); at the time of this study, the separate ranges of *C. novaeguineae* and *C. halli* were unknown, and the taxonomic validity of *C. halli* has been brought into question by Agne *et al.* (2026)]. D, approximate modern distribution of *Crocodylus johnstoni* [based on Isberg *et al.* (2017)]. Locality numbers: (1) Hayne's Cave, Campbell Island, Montebello Island Group, Western Australia (Veth *et al.* 2007, Manne and Veth 2015); (2) Ngalanguru (High Cliffy Island), Western Australia (O'Connor 1994); (3) Widgingarri Shelter 1, Kimbereley, Western Australia (O'Connor 1999); (4) *Bandilngan* (Windjana Gorge), Western Australia (Gorter and Nicoll 1978); (5) Anbangbang I, Northern Territory (Foley 1985); (6) Nawarla Gabarnmang, Arnhem Land Plateau, Northern Territory (David *et al.* 2017); (7) Lake Eyre Basin localities, South Australia (Tedford and Wells 1990); (8) Terrace Site, Riversleigh, Queensland (Willis and Archer 1990, Willis and Molnar 1997a, Ristevski *et al.* 2020); (9) Floraville Downs Station, Queensland (Willis and Molnar 1997a, Molnar *et al.* 2017, Price *et al.* 2019, Ristevski *et al.* 2019, Stein *et al.* 2020); (10) Mabuyag, Torres Strait (McNiven *et al.* 2015); (11) S354/7, Princess Charlotte Bay, Queensland (Cribb and Minnegal 1989); (12) Chillagoe-Mungana region, Queensland [tentative crocodylian remains reported by David (1987)]; (13) South Walker Creek, Queensland (Hocknull *et al.* 2020); (14) King Creek and Cliffton, Darling Downs, Queensland (Sobbe *et al.* 2013, Ristevski *et al.* 2023a); (15) Andarewa Cave, Fakfak Regency, West Papua (Mene *et al.* 2025); (16) Island of Eloaua, Mussau Islands, Papua New Guinea (Kirch 2021a); (17) Panakiwuk, New Ireland (Allen *et al.* 1989, Leavesley 2004); (18) Orokolo Bay, Papua New Guinea (Basiaco *et al.* 2020); (19) Koumac, Grande Terre, New Caledonia (Balouet 1991); (20) Pindai Caves, Grande Terre, New Caledonia (Balouet and Buffetaut 1987, Anderson *et al.* 2009, Salisbury et al. 2010); (21) Nessadiou, Grande Terre, New Caledonia (Balouet 1991); (22) Kanumera, Isle of Pines, New Caledonia (Buffetaut 1983, Balouet and Buffetaut 1987); (23) Arapus and Teouma, Efate, Vanuatu (Mead *et al.* 2002, Hawkins 2015, Husdell *et al.* 2023); (24) Volivoli Cave, Viti Levu, Fiji (Molnar *et al.* 2002); (25) Wainibuku Cave, Viti Levu, Fiji (Molnar *et al.* 2002; note that it is unclear if the age of the Wainibuku Cave material is late Pleistocene or Holocene, although the latter may be more plausible); (26) Naigani, Viti Levu, Fiji (Irwin *et al.* 2011). Basemap modified from Natural Earth (www.naturalearthdata.com).

supplementary note 7 in Hocknull *et al.* (2020)]. All other specimens are thus inferred to be late Pleistocene or of an ambiguous age. For a summary of reported dates in the published literature, see Table 1.

Paludirex: *Paludirex* Ristevski *et al.*, 2020 is a mekosuchine genus containing two recognized species from the Plio-Pleistocene of mainland Australia (Ristevski *et al.* 2020, 2023a, Campbell *et al.* 2021). The type species, *P. vincenti* Ristevski *et al.*, 2020, has a fossil record spanning from the Pliocene to the Pleistocene and is represented by relatively complete skull material that provides the basis for most morphological information on this taxon. The Pleistocene record of *P. vincenti* is best exemplified by QMF1752 (informally called the 'Lansdowne snout' after Lansdowne Station, the locality of its discovery; see Longman 1925), an incomplete skull that was recently assigned to *P. vincenti* (for details, see: Ristevski *et al.* 2020 and 2023a). The suggested Pleistocene age of QMF1752 is inferred from other fossil material found at Lansdowne Station, which contains Pleistocene taxa such as the marsupials *Palorchestes azael* Owen, 1873 and *Protemnodon anak* Owen, 1874 (see: Longman 1925, Willis and Molnar 1997a). However, the exact age of QMF1752 is unknown and could be

Table 1. Summary of known dates for Australasian crocodylians from the past 50 kya, as reported in the currently published literature. Note that only one specimen has been directly dated (~20000 years BP, Mekosuchinae gen. et sp. indet. from South Walker Creek). Ages for all other taxa and specimens are inferred based on dating of their localities of origin. Ages for some specimens and taxa are unknown. Note that some specimens of *Mekosuchus inexpectatus* and *Volia athollandersoni* have been inferred as late Pleistocene, although exact ages remain unknown (e.g. Molnar *et al.* 2002, Holt *et al.* 2007).

Taxon	**Location/Site**	**Reported age (years ago)**	**Sources**
Crocodylus sp. indet.	Nawarla Gabarnmang, Northern Territory, Australia	<300	David *et al.* (2017)
Crocodylus sp. (eggshell)	Anbangbang I, Northern Territory, Australia	<300	Foley (1985)
Crocodylus sp. cf. *C. porosus*	Widgingarri Shelter 1, Western Australia, Australia	<300	O'Connor (1999)
Crocodylus porosus	Mabuyag, Torres Strait, Australia	~100–500	McNiven *et al.* (2015)
Crocodylus sp. indet.	Orokolo Bay, Papua New Guinea	540–285	Basiaco *et al.* (2020)
Crocodylus porosus	Panakiwuk, New Ireland, Papua New Guinea	1600–640	Marshall and Allen (1991)
Mekosuchus inexpectatus	Pindai Caves, Grande Terre, New Caledonia	1720 ± 70	Balouet and Buffetaut (1987)
Crocodylus porosus	Eloaua, Mussau Islands, Papua New Guinea	2853–2775	Kirch (2021a)
?*Volia athollandersoni*	Naigani, Viti Levu, Fiji	~2900–2700	Irwin *et al.* (2011)
Mekosuchus kalpokasi	Teouma, Efate, Vanuatu	2960–2710	Hawkins (2015)
Mekosuchus kalpokasi	Arapus, Efate, Vanuatu	~3000	Mead *et al.* (2002)
Mekosuchus inexpectatus	Kanumera, Isle of Pines, New Caledonia	3750 ± 210	Balouet and Buffetaut (1987)
Crocodylus porosus	Andarewa Cave, West Papua	5286–4970	Mene *et al.* (2025)
Crocodylus porosus	Hayne's Cave, Spit 6, Campbell Island, Western Australia, Australia	7930 ± 20	Veth *et al.* (2007), Manne and Veth (2015)
Crocodylus porosus	Hayne's Cave, Spit 7, Campbell Island, Western Australia, Australia	8240 ± 90	Veth *et al.* (2007), Manne and Veth (2015)
Crocodylus porosus	Arnhem Land rock art, Northern Territory, Australia	9000–7000	Chaloupka (1983, 1984)
Crocodylus porosus	Panakiwuk, New Ireland, Papua New Guinea	10000–8000	Leavesley (2004)
Volia athollandersoni	Volivoli Cave, Viti Levu, Fiji	20000–10000	Anderson *et al.* (2001), Worthy and Anderson (2009)
Crocodylus johnstoni	Arnhem Land rock art, Northern Territory, Australia	20000	Chaloupka (1983, 1984)
Mekosuchinae gen. et sp. indet.	South Walker Creek, Queensland, Australia	~20000	Hocknull *et al.* (2020)
Crocodylus johnstoni	Terrace Site, Riversleigh, Queensland, Australia	28000–21000*	Willis and Archer (1990), Davis and Archer (1997)
Paludirex gracilis	Terrace Site, Riversleigh, Queensland, Australia	28000–21000*	Davis and Archer (1997), Willis and Molnar (1997a)
Crocodylus sp. cf. *C. porosus*	South Walker Creek, Queensland, Australia	~40100	Hocknull *et al.* (2020)
Crocodylus sp. cf. *C. porosus*	South Walker Creek, Queensland, Australia	~47700	Hocknull *et al.* (2020)

*Indicate uncertain reliability of ages (see Price *et al.* 2013).

either middle or late Pleistocene (Ristevski *et al.* 2023a). Because of this, a *P. vincenti* late Pleistocene record remains uncertain.

The second recognized species of *Paludirex*, *P. gracilis* (Willis and Molnar 1997a), is poorly known compared to *P. vincenti* due to the more fragmentary nature of its remains. The two specimens currently assigned to *P. gracilis* are the holotype premaxilla (QMF17065; Fig. 2A, B) and a fragment of a left dentary (QMF17066), both of which were discovered at the Terrace Site of the Riversleigh World Heritage Area. Radiocarbon dating of charcoal from a basal bone-bearing layer of the Terrace Site has indicated a late Pleistocene age (23900 + 4100 −2700 BP; Davis and Archer 1997). Although the *P. gracilis* specimens have not been directly dated, their late Pleistocene age has been assumed based on the radiocarbon ages associated with the Terrace Site (Willis and Molnar 1997a, Ristevski *et al.* 2020). If this reflects an accurate age estimate for the *P. gracilis* holotype, it would imply *P. gracilis* is the geologically youngest named and described mekosuchine from mainland Australia. However, the reliability of the radiocarbon ages is questionable (Price *et al.* 2013) and so the age of the Terrace Site and, by extension, *P. gracilis* are not sufficiently robust, making it possible that they could be much older.

Fragmentary fossil material from *Bandilngan* (also known as Windjana Gorge) in Western Australia may also be referable to *Paludirex*. The *Bandilngan* material was first reported by Gorter and Nicoll (1978) and includes several fragmentary fossils, the most notable of which is a partial left premaxilla (CPC 17122). This material was originally referred to as ?*Crocodylus* sp. indet. by Gorter and Nicoll (1978), although it was later identified as mekosuchine by Willis and Molnar (1997a) who referred it to the now *nomen dubium* genus '*Pallimnarchus*' De Vis, 1886 (see also: Willis 1997a, 2006). As some of the material historically assigned to '*Pallimnarchus*' is now referred to *Paludirex* (see: Ristevski *et al.* 2020), it is possible that the *Bandilngan* fossils may also belong to this genus. Regarding the age of the *Bandilngan* crocodylian, Gorter and Nicoll (1978: 97) vaguely suggested a '…post-Miocene age' and 'If the deposit is correlated with the Warrimbah Conglomerate (Veevers and Wells 1961) the age is no younger than late Pleistocene' (see also: Gorter and Nicoll 1978: 104). Despite a proposed late Pleistocene age, Gorter and Nicoll (1978: 104) also noted that '…an Early Pleistocene age cannot be discounted' and even that '…the fossil site may be as old as Early Miocene'. Ultimately, Gorter and Nicoll (1978: 104) assigned the age of the *Bandilngan* fossil site as probably Late Cenozoic. Given the morphological similarities of CPC 17112 with *Paludirex* spp. and the fact that this genus has a temporal range of Pliocene–late Pleistocene, it is possible that the *Bandilngan* fossils are indeed late Quaternary in age. However, without direct dating of the specimens, it remains unclear if this material is indeed late Pleistocene or perhaps older. Hence, the late Pleistocene assignment of the *Bandilngan* material must be considered tentative for the time being.

Ziphodont mekosuchines: Perhaps the most distinctive crocodylians from the Quaternary of Australia were the mekosuchines with ziphodont dentition (i.e. labiolingually compressed and serrated teeth). Although ziphodont crocodyliforms inhabited the Americas, Africa, and Eurasia at various points during the Cenozoic, Australasia—specifically New Guinea and mainland Australia—remained the only region on the planet where ziphodont crocodyliforms persisted into the Pleistocene [see Ristevski *et al.* (2025) for an overview of Cenozoic ziphodont crocodyliforms]. Based on a combination of morphological features, ziphodont mekosuchines are hypothesized to have been primarily terrestrial hunters (e.g. Molnar 1982a, Willis *et al.* 1990, Flannery 1994, Megirian 1994, Willis 1997a, 2006). Fossil remains of ziphodont crocodylians referable to Mekosuchinae are best known from mainland Australia, whereas the New Guinean record dating to the late Pliocene is much more fragmentary in comparison (Plane 1967, Ristevski *et al.* 2025). At present, *Quinkana* Molnar, 1982a is the only named ziphodont mekosuchine genus and contains four established species spanning from the Oligocene to the Pleistocene (Molnar 1982a, Megirian 1994, Willis and Mackness

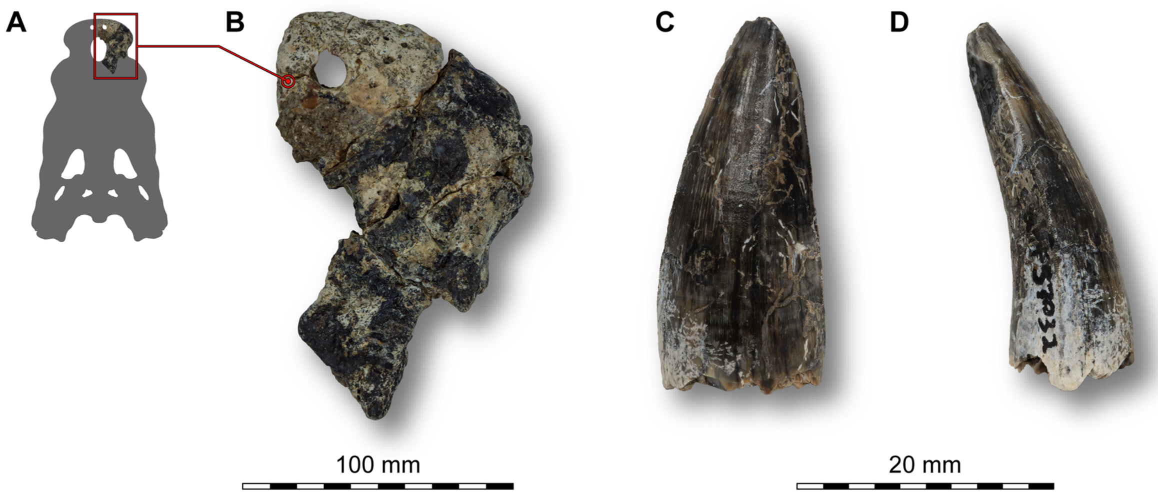

Figure 2. Examples of late Pleistocene mekosuchine remains from mainland Australia. A, hypothetical skull silhouette of *Paludirex gracilis* with the inset highlighting the anatomical position of the holotype specimen (QMF17065) in (B), a right premaxilla in dorsal view. QMF57032, an isolated ziphodont tooth crown in: C, labial; D, mesial views. Hypothetical skull silhouette of *Paludirex* in (A) modified from Ristevski *et al.* (2020).

1996, Willis 1997b). Currently, ziphodont mekosuchine remains from the late Pleistocene have been reported from three palaeontological sites in Queensland—Floraville Downs Station, South Walker Creek, and King Creek (Sobbe *et al.* 2013, Molnar *et al.* 2017, Price *et al.* 2019, Ristevski *et al.* 2019, Hocknull *et al.* 2020). Most of this material is represented by isolated ziphodont teeth (Sobbe *et al.* 2013, Hocknull *et al.* 2020), although more complete material belonging to a yet unnamed taxon from Floraville Downs exists (Molnar *et al.* 2017, Price *et al.* 2019, Ristevski *et al.* 2019). The ziphodont mekosuchine material from South Walker Creek represents the geologically youngest ziphodont crocodylomorph material known (Hocknull *et al.* 2020). A single isolated ziphodont tooth crown from King Creek in the Darling Downs, QMF57032, represents the southernmost known record of ziphodont crocodylians from the late Pleistocene (Figs 1, 2C, D). Although no direct dating has been performed on QMF57032, its age is considered late Pleistocene based on other deposits from the area (Price and Sobbe 2005, Price and Webb 2006, Price *et al.* 2011). Additional ziphodont crocodylian remains are known from several Pleistocene localities in Australia; however, because their exact ages are unknown, they are not included in this report (for additional information, see: Molnar 1982a, Ristevski *et al.* 2023a, 2025). Due to the relative rarity and highly fragmentary nature of ziphodont crocodylian remains from the Pleistocene, the taxonomy for much of this material is unclear and not all of it belongs to the genus *Quinkana*. Future assessments along with potential new discoveries are necessary to clarify the taxonomy of ziphodont crocodylians from the Quaternary.

Other mekosuchine material: Additional crocodylian specimens that are potentially late Pleistocene in age are known from the Darling Downs in south-eastern Queensland. One such specimen is NHMUK PV OR 43047a, material belonging to a proportionally broad-snouted and non-ziphodont crocodylian that, according to museum records, was recovered near the town of Clifton in the Darling Downs. This specimen was discussed and presented in Ristevski *et al.* (2023a), where it was provisionally referred to as the 'Darling Downs taxon'. The age of the crocodylian(s) from the Clifton area is uncertain but, based on its provenance, it is possible that it is late Pleistocene.

As mentioned above, there is currently only one crocodylian specimen that has been directly dated—QMF59869—an isolated conidont tooth crown from South Walker Creek that is estimated to date to ~20 kya [supplementary note 7 in Hocknull *et al.* (2020)], making it the youngest reliably dated mekosuchine specimen from mainland Australia. Originally, QMF59869 was assigned to the genus '*Pallimnarchus*', although this taxonomic referral predates the taxonomic revision of '*Pallimnarchus*', where it was declared a *nomen dubium*. While it is possible that QMF59869 may belong to *Paludirex*, without clarifying the taxonomy of other broad-snouted and non-ziphodont mekosuchines such as the 'Darling Downs taxon', there is a possibility that QMF59869 may be referable to a different genus than *Paludirex*. As such, we suggest that QMF59869, as well as other material from South Walker Creek that was assigned to '*Pallimnarchus*', be temporarily referred to as Mekosuchinae gen. et sp. indet. until the taxonomy of non-ziphodont Plio-Pleistocene mekosuchines is better understood.

Tedford and Wells (1990) reported late Pleistocene vertebrate fossils, including crocodylians, from several deposits in the eastern Lake Eyre Basin, exposed along the courses of the Warburton River and Cooper Creek in the Tirari Desert. The most common crocodylian elements reported by Tedford and Wells (1990) were teeth and osteoderms, although other material, such as craniomandibular and additional postcranial elements, were mentioned by those authors as well. These deposits rest upon, or are incised into, the main body of the Tirari Formation, which is accepted as Pliocene in age (Tedford *et al.* 1992, Megirian *et al.* 2010). The sequence above the main body of the Tirari Formation consists of a series of fluviatile channels capped with aeolian sands and palaeosols. There are three named units, the oldest being the Pompallina Member of the Tirari Formation, which is thought to be late Pliocene in age (Tedford *et al.* 1992), the Kujitara Formation, which is possibly middle Pleistocene (Tedford and Wells 1990), and the upper Pleistocene Katipiri Formation. However, each of these units consists of multiple stacked channels covering a range of ages. The relevant formation here is the Katapiri Formation, which contains channel fill from two main depositional phases: an earlier phase approximately 270–220 kya and a late Pleistocene phase at approximately 120 to 90 kya, based on luminescence dating (Callen and Nanson 1992, Nanson *et al.* 1992, Maroulis *et al.* 2007). None of the crocodylian material from the Katipiri Formation can be traced to a directly dated channel, so the possibility remains that none of it dates to the late Pleistocene. Some of the material was interpreted as *C. porosus* by Tedford and Wells (1990: 275, 276, 278); however, this identification necessitates re-inspection considering significant advances in crocodylian palaeontology since 1990. Among the specimens referred to *C. porosus* by Tedford and Wells is a crushed posterior portion of a skull with mandibles that could potentially derive from the Katapiri Formation. This specimen has been re-examined and found to belong to a yet unnamed species of *Crocodylus* (Yates 2019). Many of the crocodylian specimens thought to derive from the Katipiri Formation, notably from Keekalanna Soak on the Warburton River and Kutjitara and Waralamanko Waterholes on Cooper Creek, are heavily mineralized, fragmentary and often bear a polished patina. Such material has probably been reworked from older middle Pleistocene or Pliocene deposits that underlie the Katipiri Formation (A. Yates and A. Camens pers. comm. 2025). In contrast, specimens from the Katapiri Formation of Malkuni Waterhole, Cooper Creek, do not show these features and may represent fossils contemporary with deposition of the Katipiri Formation and thus could potentially be late Pleistocene in age. Specimens from this site consist mostly of isolated conidont tooth crowns. Some of these isolated teeth have fluted enamel surfaces, whereas others do not. Conidont crocodylian teeth without fluted enamel are typical of mekosuchines (e.g. *Australosuchus clarkae* Willis and Molnar, 1991, species of *Baru* Willis *et al.*, 1990, species of *Kambara* Willis *et al.*, 1993, species of *Paludirex*, and the 'Darling Downs taxon') but not species of *Crocodylus*, which tend to possess fluted teeth (see: Willis and Molnar 1997b, Buchanan 2009, Yates 2017, Ristevski 2019, Ristevski *et al.* 2020, 2025, Yates *et al.* 2023). Therefore, it appears that at least some of these Lake Eyre Basin specimens are mekosuchine in origin, some belong to the genus *Crocodylus*, whereas other material may not be diagnostic beyond

Crocodylia. Additional comments cannot be made until a detailed study of this material is completed.

The late Quaternary mekosuchine record from the south-west Pacific

Mekosuchus: The genus *Mekosuchus* Balouet and Buffetaut, 1987 includes four named species, two of which are Quaternary in age—*M. inexpectatus* Balouet and Buffetaut, 1987 from New Caledonia and *M. kalpokasi* Mead *et al.*, 2002 from Vanuatu. These were small-bodied mekosuchine crocodylians (approximate total length estimates of under 2 m at maturity; Fig. 3) with proportionally short snouts and blunt posterior teeth suited for crushing bites (for a review, see also: Ristevski *et al.* 2023a). Material of *M. inexpectatus* is mainly known from the Pindai Caves on the island of Grande Terre and the Kanumera locality on the Isle of Pines, most of which is currently undescribed (Fig. 4A; Balouet and Buffetaut 1987, Balouet 1989, 1991, Salisbury *et al.* 2010). Original age estimates of the Pindai and Kanumera material were suggested to be Holocene, although a late Pleistocene age has been proposed by some authors (Willis 2006, Holt *et al.* 2007; Table 1). Anderson *et al.* (2009: 108) stated that 'there is no case as yet for human coexistence with, or human impact upon…' *Mekosuchus* on New Caledonia. Additional fragmentary material referred to *Mekosuchus* by Balouet (1989, 1991) was also reported from archaeological localities in Koumac and Nessadiou on Grande Terre. The sites at Koumac and Nessadiou also contain pottery of Lapita settlers (e.g. Frimigacci and Siorat 1988, Siorat 1992, Sand 2007), suggesting human temporal overlap with, and utilization of, *M. inexpectatus*. Flannery (1994: 48) also mentioned that a jawbone was found at an old village site in New Caledonia, which would further support the utilization of *M. inexpectatus* by humans. However, it must be pointed out that no further details were provided by Flannery (1994) as to what was meant by 'old village site' and why the mentioned jawbone was interpreted as belonging to *M. inexpectatus*; this specimen is, therefore, in need of in-depth assessment.

Mekosuchus kalpokasi is known from fragmentary remains recovered at Holocene archaeological sites (Mead *et al.* 2002, Hawkins 2015). The holotype of *M. kalpokasi*, an incomplete left maxilla (UF 162724; Fig. 4C–E), was discovered at the immediately post-Lapita archaeological site of Arapus on the island of Efate, Vanuatu (Fig. 1). In addition to the holotype, Mead *et al.* (2002) also referred two fragmentary limb elements to this taxon. Radiocarbon dating of shells from the Arapus site suggested the age of the *M. kalpokasi* material to be between 3200 and 2706 years cal. BP (Mead *et al.* 2002). Fragmentary dental, dermal, vertebral, and limb elements are known from a second archaeological site on Efate proximal to Teouma Bay (Hawkins 2015, Husdell *et al.* 2023), although these were categorized by Hawkins (2015) only as Crocodyloidea. Most of the *M. kalpokasi* remains were found in the basalmost layer dated 2960–2710 cal. BP (Hawkins 2015). The remainder came from an adjacent midden estimated to be the same age. At least three individuals are represented by this material which is yet to be formally published (Husdell *et al.* 2023).

Volia: *Volia athollandersoni* Molnar *et al.*, 2002 is a mekosuchine from the late Pleistocene–Holocene of Fiji and is the only recognized crocodylian endemic to this island group. All currently known material of *V. athollandersoni*, which is fragmentary (Molnar *et al.* 2002; see also: Worthy *et al.* 1999, Worthy and Anderson 2009, Ristevski *et al.* 2023a), comes from the island of Viti Levu (Figs 1, 4B). The Viti Levu material was recovered from two caves: the Wainibuku and Volivoli Caves (the latter also spelled as Voli Voli; e.g. Molnar *et al.* 2002). No direct dating has been attempted on the crocodylian remains, although preliminary dates for the fossiliferous clay of the Volivoli Cave (specifically Volivoli #1) indicated an age range of 10000–20000 years BP (Anderson *et al.* 2001). Based on this, the age of the Volivoli Cave material has been presumed to be late Pleistocene (Molnar *et al.* 2002). The age of the Wainibuku Cave material was also presumed Pleistocene by Molnar *et al.* (2002), although these authors did

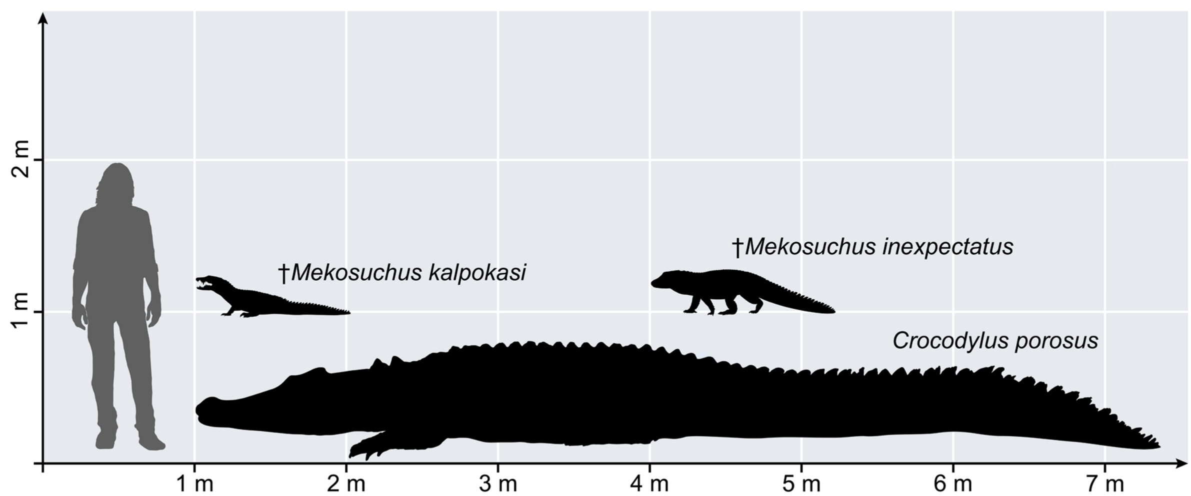

Figure 3. Size comparisons between the largest and smallest known crocodylian species from the late Quaternary of Australasia. Silhouette of *Mekosuchus kalpokasi* is scaled based on the size of the holotype maxilla (UF 162724). Silhouette of *Mekosuchus inexpectatus* is scaled based on the size of the holotype mandible (NCP 06). Silhouette of *Crocodylus porosus* is scaled after the largest measured specimen (skin) of 6.2–6.3 m in total length (Whitaker and Whitaker 2008). † indicates extinct.

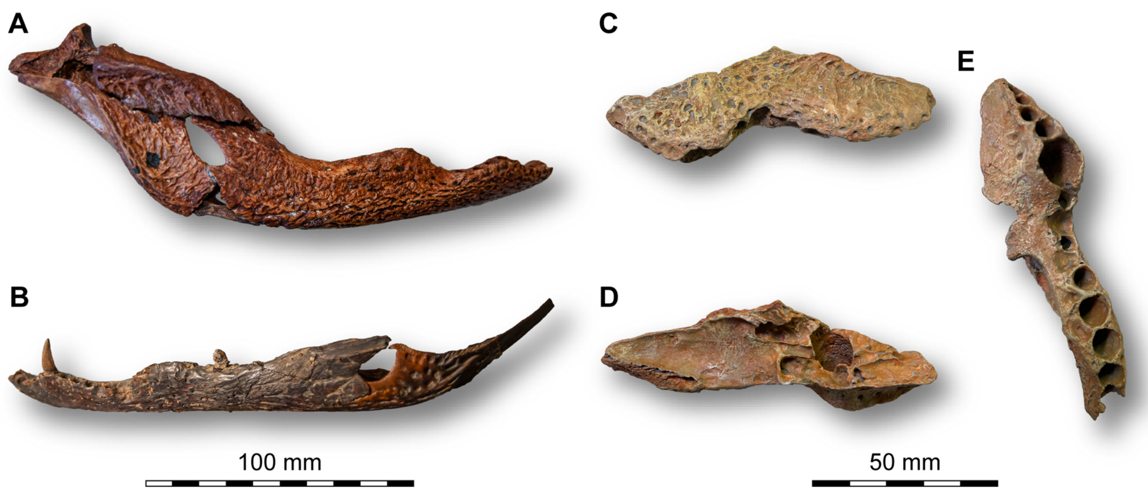

Figure 4. Examples of late Quaternary mekosuchine remains from the south-west Pacific. A, *Mekosuchus inexpectatus*, NCP 06, holotype, right mandible in lateral view. B, *Volia athollandersoni*, NMNZ S37332, partial left mandible in lateral view. *Mekosuchus kalpokasi*, cast of UF 162724, holotype, left maxilla in: C, lateral; D, medial; and E, ventral views. Modified from Ristevski *et al.* (2023a).

not exclude the possibility that it may be more recent. Others have suggested that material from the Wainibuku Cave is '…probably Holocene, as the fossils were in unconsolidated sediments adjacent to an intermittently active stream' (Worthy 2000: 344).

Highly fragmentary crocodylian material is also known from the small island of Naigani, Fiji (Irwin *et al.* 2011). The Naigani crocodylian is represented by an osteoderm, an isolated and worn tooth crown, and a cranial fragment, which were only tentatively assigned to *V. athollandersoni* by Irwin *et al.* (2011). Nevertheless, due to their fragmentary condition and poor diagnostic utility, Irwin *et al.* (2011) also considered the possibility that they could instead belong to *C. porosus*, which does not have a permanent population on Fiji but is within the range of the species (Grigg and Kirshner 2015). The Naigani material is of Holocene age, having been recovered from a Lapita site (VL 21/5) where radiocarbon dating indicates human settlement began around 2900 years BP, lasting for a brief period probably ending between 2700 and 2750 years BP (Irwin *et al.* 2011). According to Irwin *et al.* (2011: 75), the crocodylian remains from Naigani were found as oven contents associated with cooking stones. Other extinct fauna from the same site reported by Irwin *et al.* (2011) includes the giant iguanid *Lapitiguana impensa* Pregill and Worthy, 2003, a large pigeon of the genus *Ducula* Hodgson, 1836, and a giant megapode of the genus *Megavitiornis* Worthy, 2000. This suggests that humans utilized the native fauna of the island, including the crocodylians (Irwin *et al.* 2011). Thus, while the last known appearance date of *V. athollandersoni* is unclear, it is likely that this crocodylian was one of the last surviving mekosuchines, and that its extinction can potentially be attributed to anthropogenic factors (Anderson 2002).

The late Quaternary record of *Crocodylus*

The Australasian palaeontological record of *Crocodylus* extends back to the Pliocene of both mainland Australia as well as New Guinea (e.g. Plane 1967, Molnar 1979, Yates and Pledge 2017, Yates 2019, Ristevski *et al.* 2025). A synthesis of the known Plio-Pleistocene record of the genus in the region was recently given in Ristevski *et al.* (2023a).

Australia

The palaeontological record: There are currently no known fossil remains that can be identified as belonging to *C. novaeguineae* (or *C. halli*, if taxonomically distinct; see: Agne *et al.* 2026), and the fossil record of *C. porosus* in the region is tentatively referred to as *Crocodylus* sp. cf. *C. porosus* (Yates 2019, Hocknull *et al.* 2020, Ristevski *et al.* 2023a). The latter is comprised of isolated teeth and osteoderms and were recovered from two sites at South Walker Creek dated to ~47.7 kya and ~40.1 kya, respectively (Hocknull *et al.* 2020; Table 1). Based on Oaks (2011), the mean molecular divergence date for *C. novaeguineae* and *C. johnstoni* is 10.06 Mya and the 95% highest posterior densities range from 7.17 to 12.41 Mya, placing the divergence of these two Australasian species in the Miocene. Additionally, results by Oaks (2011) support an Australasian origin for *Crocodylus* during the Miocene. Presumably, the Miocene origin of at least *C. johnstoni* and *C. novaeguineae* is, therefore, in Australasia, although no fossil record is known for either of these going that far back.

The most complete fossil remains of *Crocodylus* from the late Quaternary Australasian record are referred to the extant *C. johnstoni*. The fossil evidence for this species is a nearly complete left dentary ramus (QMF13115) from the Terrace Site in Riversleigh, which is also the type locality of *P. gracilis*. Specimen QMF13115 was assigned to *C. johnstoni* by Willis and Archer (1990), who found its morphology to be nearly indistinguishable from the extant species. However, Willis and Archer (1990) noted three minor morphological differences between QMF13115 and their comparative sample of *C. johnstoni*, but they ultimately concluded that these are most parsimoniously interpreted as intraspecific variations.

The archaeological record: Several archaeological sites from Australia have yielded fragments that are referable to the extant species of *Crocodylus*. All these sites are coastal or near-coastal and, except for one, are in regions that in post-European colonial history and today host permanent populations of *C. porosus* or *C. johnstoni*, or both (Fig. 1). Foley (1985) documented a crocodile eggshell at

Anbangbang 1 in Kakadu, Northern Territory, which, along with most other reptile remains at the site, probably represent subsistence remains. Another instance from the recent archaeological record (less than 300 years old) of Arnhem Land in the Northern Territory comes from David *et al.* (2017) who reported a maxillary fragment interpreted to have belonged to a ~1-m long crocodile. David (1987) reported tentative crocodile fragments from a late Holocene archaeological site in the Chillagoe-Mungana region, north Queensland, that may reflect consumption by humans. Crocodile remains have also been reported from Ngalanguru (High Cliffy Island) in the Kimberley, Western Australia (O'Connor 1994). The crocodile material from Ngalanguru was accompanied by other faunal remains including a '…large quantity of turtle and dugong bone as well as fish…' with the crocodile material attributed to *C. porosus* (O'Connor 1994: 105).

Relative to other mainland archaeological sites, Widgingarri Shelter 1 stands out as one of the richest in crocodile remains (O'Connor 1999). Situated on the mainland, north-west of Ngalanguru (Fig. 1), the site yielded a total of 11 specimens identifiable as crocodylian, all of which are highly fragmentary (Fig. 5). Some of the elements cannot be determined as to which part of the skeleton they derive from, although some could be identified as fragments of a premaxilla and jugal that are probably referable to *C. porosus* (Fig. 5E–G).

Finally, the early Holocene archaeological site of Hayne's Cave on Campbell Island, in the Montebello Islands, ~80 km offshore from the Pilbara, Western Australia, also presented evidence of crocodylians (Fig. 1). This material consists of two *C. porosus* teeth that were first reported by Veth *et al.* (2007) and subsequently by Manne and Veth (2015). Today, there is no permanent population of *C. porosus* or any other crocodylian that inhabits the region near Campbell Island. Veth *et al.* (2007) suggested that these teeth may indicate that during the early Holocene, *C. porosus* distribution extended much further south than it does today. Alternatively, Manne and Veth (2015) suggested that the early Holocene *C. porosus* from Hayne's Cave may instead be from a vagrant individual or individuals.

Torres Strait: The only known archaeological record of crocodylians from the Torres Strait comes from the island of Mabuiag (McNiven

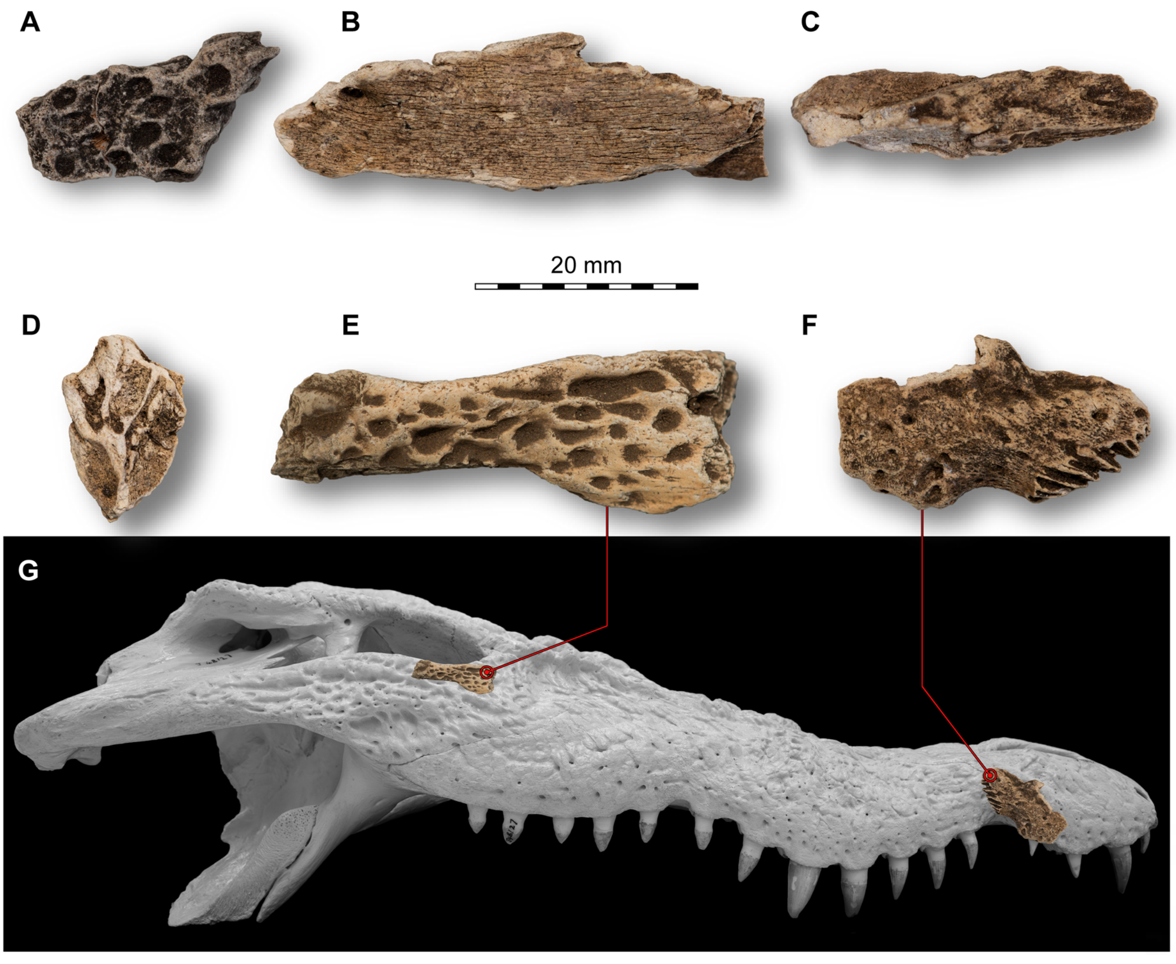

Figure 5. Examples of Holocene crocodylian remains from the Widgingarri Shelter 1 archaeological site on mainland Australia. A, undetermined fragment of *Crocodylus* sp. cf. *C. porosus* from Widgingarri Shelter 1, Square AA, Spit 3. B–D, undetermined fragments of *Crocodylus* sp. cf. *C. porosus* from Widgingarri Shelter 1, Square D, Spit 3. E, right jugal fragment of *Crocodylus* sp. cf. *C. porosus* from Widgingarri Shelter 1, Square D, Spit 1 in lateral view. F, left premaxillary fragment of *Crocodylus* sp. cf. *C. porosus* from Widgingarri Shelter 1, Square D, Spit 3 in lateral view. G, the right jugal and left premaxillary fragments from (E) and (F) superimposed on a *Crocodylus porosus* skull (QMJ48127) for anatomical reference [not to scale; note that the left premaxillary fragment (F) has been mirrored to aid comparison].

et al. 2015). Mabuiag (also known as Mabuyag) is a small island in central western Torres Strait, Queensland, where crocodiles have important cultural (totemic) significance (Haddon 1904: ch. 4, Lui-Chivizhe 2022, Wright 2011). The material reported from Mabuiag was discovered in a late Holocene midden (~100–500 years cal. BP; McNiven *et al.* 2015) and comprises seven (mostly caudal) vertebrae from one or more small individuals of *Crocodylus* sp.. These crocodile vertebrae may indicate that the animal(s) were killed for food, although considering their small number, McNiven *et al.* (2015) did not exclude the possibility that these may represent the remains of a naturally deceased animal. The *Crocodylus* material reported from Mabuiag is significant because it is the first and thus far only reported finding of a crocodile from an archaeological site in the Torres Strait. Due to their fragmentary nature, precise specific identification for these vertebrae was not provided by McNiven *et al.* (2015), but given their location and recent age it is very likely that they belong to *C. porosus*, which is the only crocodylian that inhabits the Torres Strait today (Webb *et al.* 2021).

New Guinea and surrounding islands

All the currently known crocodylian records from the late Quaternary of New Guinea and surrounding islands are Holocene and can be attributed to *Crocodylus*. Four archaeological sites have reported crocodile material: two on mainland New Guinea and two on nearby islands (Fig. 1). Papua New Guinea holds three of the four records, with the first coming from Orokolo Bay in the Papuan Gulf, where Basiaco *et al.* (2020) reported small fragments referable to *Crocodylus* sp. dated to 540–285 years cal. BP. The other two records from Papua New Guinea come from islands of the New Ireland Province.

A single vertebra from the archaeological site of Talepakemalai (Site ECA) on the island of Eloaua, Mussau Island Group, was reported by Kirch (2021a). This vertebra was estimated to have belonged to an individual with a total length of 2 m (Kirch 2021a) and derives from a Holocene unit with a calibrated age range of 2853–2775 years BP (Kirch 2021b). *Crocodylus porosus* is the only crocodylian that inhabits the mangrove swamps of Mussau and is the most likely species to which the vertebra from Talepakemalai belongs. Kirch (2021a: 169) noted that the inhabitants of Mussau '... expressed a healthy respect for these formidable creatures. It is not surprising, therefore, that they were never extensively hunted for food' (see also: Kirch and Catterall 2021: 34).

The other archaeological site from New Ireland Province with reported crocodylian fragments is Panakiwuk Cave on the island of New Ireland [Allen *et al.* 1989, Marshall and Allen 1991, Leavesley 2004; it should be noted that Marshall and Allen (1991) tentatively identified the remains as crocodylian, referring to them as ?*Crocodylus* sp.]. All reported crocodile fragments originate from Holocene deposits, with the oldest coming from deposits dated to between 10000 to 8000 years BP, and more recent ones from layers dated to 1600 to 640 years bp (Marshall and Allen 1991). The presence of these remains alongside fish bones, shellfish, and marine turtle remains suggests that crocodiles were part of the coastal fauna utilized by humans.

Most recently, Mene *et al.* (2025) presented evidence of crocodylians from an archaeological site at Andarewa Cave in the Bomberai Peninsula of West New Guinea. It consists of an isolated tooth preserving the complete crown along with its root. Importantly, this tooth has a circular perforation near the base of the root, indicating that it was most likely used as an ornament by people, with Mene *et al.* (2025) suggesting it was probably part of a necklace. Usage of crocodile teeth for decorative purposes in Australasia is also documented in modern times. For example, crocodile teeth are known to have been used as hair ornaments in north-western Australia (Thomson 1948). Based on the photographs of the tooth provided by Mene *et al.* (2025), the crown is conical and appears to have fluted enamel surface which is morphologically consistent with teeth of extant *Crocodylus*.

Crocodylian representation in rock art

Rock art depicting crocodylians has been documented throughout northern Australia and been produced by many different Indigenous communities and cultural groups. Virtually all depictions have been interpreted as representations of *C. johnstoni* or *C. porosus* by archaeologists (see summary of published literature below). Crocodylians have been a recurring motif in Australian rock art from the late Pleistocene to modern times (e.g. Chaloupka 1984, Taçon *et al.* 2023). At present, there is no recognized rock art that is known to represent mekosuchines. Nevertheless, crocodylian rock art has served as inspiration in mekosuchine palaeontology. Molnar (1982a) referred to the mythological Quinkan spiritual beings who are associated with rock art sites in Cape York, North Queensland, as an etymological basis for the genus *Quinkana* (Trezise 1971, 1977; J. Ristevski and R. Molnar pers. comm. 2025). One of these rock art sites, called the Quinkan Gallery, contains depictions of crocodiles (Trezise 1977).

Trezise (1977) authored the most detailed publication dedicated exclusively to crocodylians in Australian rock art. It detailed 35 Laura rock art depictions of crocodiles from across 20 sites in 'Quinkan Country' on Cape York (also referred to as 'Laura Art' in the archaeological literature due to it being in the Laura Sandstone Basin and near the town of Laura in northern Queensland; e.g. Trezise 1977, Rosenfeld 2010, Cole 2022). All of these are stylized depictions of crocodiles shown from a dorsal aspect with the limbs splayed out to the side of the body, typical of depictions of other animals with proportionally short limbs, such as lizards, tortoises, and monotremes (Trezise 1977). Anatomical details are intermittently presented in the 'Laura Art' crocodiles, with some depictions having the eyes, teeth, toes, and tail whorls/serrations included [Trezise (1977) noted that anatomical accuracy is variable, as some paintings have an incorrect number of digits when compared to the real-life animals], whilst three are X-ray-style paintings that show the internal organs of the imaged animal. Most of the paintings have a monochrome base-colour with a contrasting contour and where the teeth and eyes are included, they are also painted with a colour that contrasts with the base. Some have painted longitudinal lines and/or dots over the body of the crocodile, which may represent the scale-and-scute patterns present in the animal. However, Trezise (1977) pointed out that line and dot patterns also adorn other animals in rock art depictions, and thus they may instead be a stylistic choice that is not meant to reflect the skin patterns and texture of a crocodile. Due to the relatively elongated and slender snouts of the crocodiles in 'Laura Art', Trezise (1977) inferred that most of these are meant to depict *C. johnstoni*, which inhabits the region (Isberg *et al.* 2017; Fig. 1).

A number of Indigenous communities from the Northern Territory are also known to have produced crocodile rock art motifs (Chaloupka 1983, 1984; see also: Kelly *et al.* 2021, Marshall *et al.* 2022). For example, Chaloupka (1983, 1984) reported on late Pleistocene and early Holocene rock art from the Arnhem Land plateau that also includes depictions of crocodiles. A late Pleistocene painting from the plateau includes a large depiction of *C. johnstoni* portrayed in dorsal view with a proportionally thin snout, limbs splayed to the side of the body, and a curved tail with details of the whorls. It dates to the proposed pre-Estuarine Stylistic Period *c.* 20000 years BP (*sensu* Chaloupka 1983, 1984; see also: May *et al.* 2017). Early Holocene rock art, associated with the proposed Estuarine Stylistic Period *c.* 9000–7000 years BP (*sensu* Chaloupka 1983, 1984; see also: May *et al.* 2017), includes rock art interpreted as portraying *C. porosus*. The proposed *C. porosus* painting depicts the animal in dorsal view with the limbs also splayed out to the sides of the body, and a curved tail carrying the whorls. The rostrum of the proposed *C. porosus* painting has a proportionally shorter snout than that in depictions of *C. johnstoni*, with the jaws agape exposing seven teeth (see: Chaloupka 1984: fig. 20).

Motta *et al.* (2020) detailed and photographed rock art from the Kimberley region in Western Australia that depicts two crocodiles. One of these is a large Wanjina Period motif of a crocodile with a white base colour and red outline that is superimposed over several anthropomorphic figures, whereas the other is a white-and-red Wanjina-style painting adjacent to depictions of macropodids. As in 'Quinkan Country' and Arnhem Land rock art, this crocodile art from the Kimberley region is also depicted from a dorsal aspect with the limbs of the crocodiles splayed out laterally. At least the motif with the white base colour displays a proportionally narrow snout with numerous pointed lines indicating the teeth along its margins and may represent *C. johnstoni*. Other mentions of crocodiles in Kimberley rock art have been made by Elkin (1930) who reported that some are depictions of *C. johnstoni*, Blundell (1974), and O'Connor *et al.* (2013), as well as a mention by Harper *et al.* (2020) of a repaint over a crocodile motif.

Outside of Australia, rock art depictions of crocodylians in the Australasian region have been reported from West Papua on the island of New Guinea. The crocodile motifs from West Papua, including their appearance, occurrence, and interpretation, have been discussed by Arifin and Delanghe (2004) and Permana and Mas'ud (2022). These are highly stylized images, with Arifin and Delanghe (2004) noting that in some cases it is difficult to distinguish between paintings of lizards and crocodiles. Permana and Mas'ud (2022) reported crocodile motifs from the Suanggini site in the Teluk Wondama Regency that were illustrated in red paint. Reptilian motifs such as crocodylians or squamate are '…considered not only the personification of ancestors but also the protectors of the entire Sentani community' (Permana and Mas'ud 2022: 191). Further regarding the cultural significance of crocodiles in West Papua and their artistic depictions, Permana and Mas'ud (2022: 191) note that '[t]he continuous depiction of lizards/monitor lizards/crocodiles is related to the hunting tradition of the Bauzi tribe in Mamberamo Regency'.

DISCUSSION

Extinctions

Although crocodylians (species of *Crocodylus*) still inhabit Australasia and are critical parts of their respective ecosystems, the extinction of mekosuchines represents a profound loss of a unique lineage, with ecological consequences for Australia and the south-west Pacific that we have yet to fully understand. Not only were mekosuchines representatives of an evolutionarily distinct group that enriched the taxonomic diversity of crocodylians during the Quaternary, but their disparate craniodental morphologies strongly suggest they occupied trophic and ecological niches that have been left vacant for millennia. The latter is especially true in the case of the altirostral ziphodont forms and the insular 'dwarf' mekosuchines, which possessed a combination of morphological features not seen among extant crocodylians. Ziphodont archosaurian reptiles have been a virtually constant component of carnivorous faunas on the planet since the Early Triassic (Nesbitt 2011), with the late Pleistocene ziphodont mekosuchines from Australia representing the last archosaurs with such a dental morphotype. The loss of these crocodylians also signifies the disappearance of a terrestrial predator type that has not been replaced in Australia since the late Pleistocene. Similar terrestrial adaptations have been inferred for the New Caledonian (and potentially Vanuatuan) species of *Mekosuchus*, and the ecological roles they fulfilled on their islands likewise remain vacant. These extinctions make Australasia one of the most severely impacted regions globally in terms of loss of crocodylian diversity.

The disappearance of apex predators like crocodylians has multiple implications for ecosystems, potentially leading to the loss and reconfiguration of biological diversity (Ordiz *et al.* 2013), reduction of ecosystem stability and resiliency, and affects to such processes and conditions as disease dynamics, carbon storage, and crop production (Ripple *et al.* 2014). Apex predators suppress mesopredators, both by killing them and motivating changes in behaviour and habitat use, and their extirpation can lead to mesopredator release, with disproportionate effects on mesopredator abundance and prey (Ritchie and Johnson 2009). Apex predators play a critical role in species' introductions, since large predators commonly limit populations of potentially irruptive introduced prey and mesopredators (Wallach *et al.* 2015).

Human occupation of Australia can be traced as far back as 65000 years BP (Clarkson *et al.* 2017). This indicates over 40000 years of potential overlap between humans and mekosuchines in Sahul (based on the U-Th dated mekosuchine material from South Walker Creek; Fig. 6). This long period of potential coexistence is not supportive of a 'blitzkrieg' extirpation of the Australian mekosuchines by humans. A rapid overkill for these crocodylians thus appears unlikely, but extended anthropogenic pressures remain plausible. Humans have had dramatic impacts on environments all over the planet (Boivin *et al.* 2016), including Australia (Legge *et al.* 2023), via alterations to fire regimes and habitats, domestication of plant and animal species, creation of novel species assemblages, alteration of biogeophysical pathways, and anthropogenic climate change (Galloway *et al.* 2008, Rosenzweig *et al.* 2008, Boivin *et al.* 2016). Many of these impacts have directly or indirectly contributed to global species' extinctions and extirpations (Dirzo *et al.* 2014, Boivin *et al.* 2016).

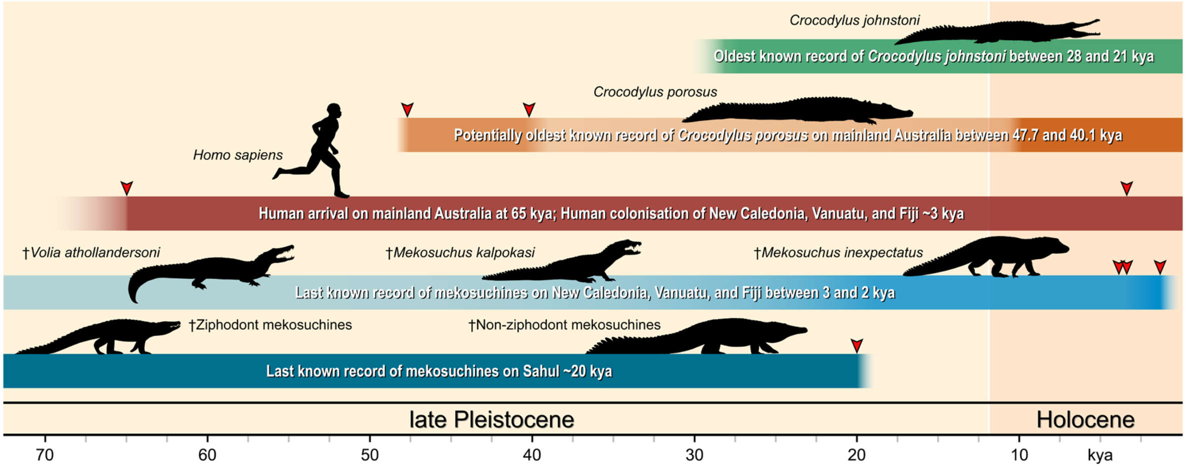

Figure 6. Chronology of key events related to crocodylian diversity and extinction in Australasia over the past 65 kya, as understood at the time of this study. Note that species of *Crocodylus* have been present in Australia and New Guinea since the Pliocene, however, their specific identification is still unclear. Therefore, the focus in this figure is on *C. johnstoni* and *C. porosus*. Red arrows indicate key individual dates (see Table 1 for details and additional dates). Solid bars indicate inferred continuous presence of taxon/taxa. Faded bars indicate uncertainties and gaps in the fossil record and known dates. Silhouettes from PhyloPic: ziphodont mekosuchine (based on *Quinkana fortirostrum*) and non-ziphodont mekosuchine (based on *Paludirex gracilis*) by Armin Reindl, and *Homo sapiens* by T. Michael Keesey. All other silhouettes by Jorgo Ristevski. † indicates extinct.

In Australia, various types of human niche construction contributed to ecological changes following the arrival of humans. Notable amongst these is cultural burning (e.g. Bliege Bird *et al.* 2008, Jones 2012), which probably shaped ecosystems in profound ways, reducing the incidence of large and destructive fires (Mariani *et al.* 2022, 2024), and altering species' abundances (Bird *et al.* 2013, 2018). Whether cultural burning also contributed to species' extirpations and extinctions in Australia remains contested (Bowman 1998, McGregor *et al.* 2010, Gammage 2011). The earliest evidence documented in the scientific literature for humans using fire to deliberately modify the landscape found in northern Australia is currently estimated at 11 000 years BP (Bird *et al.* 2024), whereas further south in Lutruwita/Tasmania, evidence for cultural burning has been dated to ~41 600 years BP (Adeleye *et al.* 2024). Thus, the potential impacts of anthropogenic fire and landscape modification on crocodylians in late Pleistocene Sahul remain uncertain, with no definitive evidence available.

Evidence of crocodylian hunting and/or food exploitation by humans in Pleistocene Sahul is likewise lacking, although it would not be without precedent given that modern Indigenous communities in Australia occasionally rely on crocodiles as a food source, such as through sustainable egg harvesting (e.g. Brockwell 1996, Brockwell 2001, Austin and Corey 2012, Bird *et al.* 2013, Corey *et al.* 2018, Saltré *et al.* 2019). While egg-harvesting activity will probably only rarely be preserved in the archaeological record, it is recognized in at least one site from the Australian Holocene (Foley 1985; also: David 1987). Trophic collapse, for example, by loss of preferred prey, may have also contributed to the extinction of mekosuchines, and a case could also be made for competitive exclusion with humans. However, the causes of the broader late Pleistocene megafaunal extinctions continue to be debated, with anthropogenic activity and climate change as the main competing explanations (e.g. Miller *et al.* 2005, Gillespie *et al.* 2006, Rule *et al.* 2012, Brook *et al.* 2013, Wroe *et al.* 2013, Sandom *et al.* 2014, Hocknull *et al.* 2020, Adeleye *et al.* 2023, Lemoine *et al.* 2023, Graipel *et al.* 2024, Perez and Prates 2024, Svenning *et al.* 2024, Archer *et al.* 2025; for review, see: Stewart *et al.* 2025).

Whether humans are the reason for the extinction of mekosuchines in Australia accordingly remains undetermined. Whilst current data are scarce, what little is known shows no evidence of direct mekosuchine utilization by humans. Indeed, the currently recognized Australian mekosuchines from the late Pleistocene were relatively large-bodied carnivorous reptiles that would have probably been dangerous to humans. It is thus reasonable to assume that the danger factor may have incentivized humans to avoid close contact with these mekosuchines, at least the large-bodied individuals but perhaps not the juveniles (note that these ideas remain purely speculative at present, as there is no evidence to support or dispute them). Why crocodylian remains only begin to appear on Australian archaeological sites in the Holocene remains unclear but may reflect increased encounters between crocodiles and people, as human populations grew, or different patterns of site use and occupation through time. However, this pattern could also reflect taphonomic factors, since *Crocodylus* remains from the sites are highly fragmented, and it may be that mekosuchine remains in archaeological sites in Australia are awaiting discovery.

Compared with Australia, the extinction of mekosuchines on New Caledonia, Vanuatu, and Fiji is arguably less elusive. Based on the known palaeontological and archaeological records, these insular mekosuchines survived into the Holocene and overlapped with humans for some time. The oldest known evidence of human occupation of the New Caledonian, Vanuatuan, and Fijian islands has been dated between 3000 and 2700 years BP (for summary, see: Bedford *et al.* 2019). It is plausible that human-introduced species, such as rats and pigs, in combination with other anthropogenic factors, like hunting and habitat alteration, may have ultimately contributed to the extinction of the small-bodied mekosuchine on New Caledonia (Balouet 1987, 1989, 1991, Flannery 1994). No known oral traditions have been recorded in the scientific literature that can be attributed to *M. inexpectatus* from New Caledonia, which supports the assumption that this species went extinct prior to European arrival on the islands (Balouet 1989). Similarly to *M. inexpectatus*, anthropogenic factors have also been suggested as the reason for the extinction of *M. kalpokasi* on Vanuatu (Hawkins 2015), with Mead *et al.* (2002: 639) stating that 'the recovery of *M. kalpokasi* in clear association with cultural debris at the Arapus site almost certainly constitutes it being food consumed by the earliest human visitors to the site'. Furthermore, Hawkins (2015) noted that one of the limb bones from Efate has rat gnawing marks, suggesting some impact by invasive species on these crocodylians. Extant crocodylians, particularly small-bodied species of *Caiman* Spix, 1825, *Osteolaemus* Cope, 1861, and *Paleosuchus* Gray, 1862 are occasionally exploited by humans for food (e.g. Ojasti 1996, Thorbjarnarson and Eaton 2004, Shirley *et al.* 2009, Grigg and Kirshner 2015; see also: Ayamba *et al.* 2024). Among extant crocodylians, the small-bodied species of *Osteolaemus* and *Paleosuchus* are morphologically most similar to the insular south-west Pacific mekosuchines. Due to their small body sizes, not only of juveniles but also mature individuals (Fig. 3), species of *Mekosuchus* would have probably posed little threat to humans, while also making them accessible as a potential food resource. Some authors have nonetheless pointed out that explicit evidence for anthropogenic involvement in the extinction of these insular mekosuchines is weak (Anderson *et al.* 2009, Slavenko *et al.* 2016). Whilst human impacts on these crocodylians is highly likely given the correlation of their disappearance with the arrival of humans, unequivocal 'smoking gun' evidence (such as mass accumulation of mekosuchine bones deposited by humans or cut marks on bones induced by human-made tools) is yet to be found. Furthermore, the palaeobiology—including, but not limited to, reproduction and nesting habits—of the insular mekosuchines is poorly understood, making current interpretations of their extinction complex, which prevents definitive conclusions. Nevertheless, evidence of crocodylians being used as food in the south-west Pacific does exist (Irwin *et al.* 2011), and humans, or at least human-induced factors such as environmental reconfiguration and introduction of invasive species, remain primary suspects for the extinction of the last mekosuchine crocodylians in this island context.

Colonization by Europeans from the late 18th century onwards created novel pressures on Australasian biodiversity, including drastic and rapid habitat loss and modification, the introduction of many exotic species and pathogens, and the disruption of traditional land management practices. Within a short timeframe, this has resulted in local extirpations and extinctions of numerous native species (e.g. Woinarski *et al.* 2015a, b, 2024, Doherty *et al.* 2016, Geyle *et al.* 2021, Roycroft *et al.* 2021, Burbidge 2023, Vakil *et al.* 2023, 2025, Llewelyn *et al.* 2025). Australia's crocodiles were also affected, especially *C. porosus*, which was intensively hunted for commercial gain to the point of becoming endangered by the mid-late 20th century (Grigg and Kirshner 2015, Walker 2016, Webb *et al.* 2021). Thanks to conservation efforts undertaken since the 1970s, *C. porosus* populations in Australia have recovered and represent a conservation success story (Webb *et al.* 2018, 2021). It is imperative that crocodile populations in the region continue to be protected as they contribute not only to ecosystem health and biodiversity, but also hold considerable cultural significance.

A fragmentary fossil record and unresolved taxonomic questions as obstacles to interpretation

The incompleteness of the fossil material leaves much of the morphology of Quaternary mekosuchines unknown and the specific identification for some fossil remains (for instance, isolated ziphodont teeth) also a mystery. Similarly, the palaeobiology of mekosuchines is poorly understood, especially in relation to their reproductive strategies, nesting behaviours, as well as their preferred prey-types. Likewise, the ranges each mekosuchine species occupied during the Pleistocene are unknown. The final extinction date for the last mekosuchines in Australia is also uncertain, and it is very likely that the youngest recognized mekosuchine fossils may not reflect the definitive extinction time for these reptiles on continental Australia. However, one of the most tantalizing questions that arises from this review is why and how did *Crocodylus* manage to survive in Australia and New Guinea, whereas mekosuchines did not? For example, fossils of both *P. gracilis* and the extant *C. johnstoni* are known from the Terrace Site at Riversleigh, and yet only one of these crocodylians persists today. The last appearance of mekosuchines in Australia is also broadly contemporaneous with the first potential appearance of *C. porosus*, especially when considering only specimens presumed to belong to the latter taxon (Ristevski *et al.* 2023a). Being apex predators, these taxa probably competed for some of the same resources, which may have impacted the persistence of mekosuchines. During the Last Glacial Maximum (LGM; between 26 and 20 kya), resources and suitable habitats were probably strained more than in previous glacial intervals as the LGM was one of the coldest periods during the Pleistocene (Williams *et al.* 2009). Unlike *C. porosus*, which inhabits a vast territory outside of the Australasian realm, semi-aquatic mekosuchine macropredators like *Paludirex* spp. appear to have been confined to Sahul, which could have made them more vulnerable than the ecologically similar *C. porosus*. To test these hypotheses, more mekosuchine material must first come to light.

The island of New Guinea is another important location for understanding mekosuchine diversity, evolution, and extinction. Thus far, crocodylian fossils are known only from the Pliocene of New Guinea and at least some of them are almost certainly referable to Mekosuchinae (Ristevski *et al.* 2025). However, given that New Guinea and mainland Australia were part of a single landmass for much of the Pleistocene, it is likely that mekosuchines also inhabited New Guinea at some point during the past 2.5 Myr. While there is no known Pleistocene mekosuchine record from New Guinea, there is nonetheless considerable potential for future discoveries.

Uncertain temporal frameworks as an obstacle to interpretation

Crocodylian fossils have been recovered from 18 Pleistocene-aged sites in Australia (see: Ristevski *et al.* 2023a). Most of this material has never been directly dated, with inferred ages based primarily on (i) the age of the site they derive from (e.g. the Terrace Site in the case of *C. johnstoni* and *P. gracilis* fossils; note that reliability of the dating methods for the Terrace Site estimates have been questioned before; see: Price *et al.* 2013); (ii) correlation with the faunal composition of their sites of origin (e.g. King Creek in south-eastern Queensland for QMF57032); and/or (iii) correlation with nearby geological deposits (e.g. the material from *Bandilngan* in Western Australia). Indeed, there are instances where crocodylian fossils were previously assigned a late Pleistocene age but are now known to be much older, such as material from Cuddie Springs. Cuddie Springs in New South Wales is well known for its Pleistocene faunal assemblages extending back approximately 900000 years, as well as for a stratigraphic sequence containing both human and megafaunal remains dated to between 40000 and 30000 years ago. Crocodylian fossils have been documented from the site (Dodson *et al.* 1993). Field and Dodson (1999) reported mekosuchine material from archaeological unit 6A at Cuddie Springs, which was subsequently dated to approximately 30000 years (Field 2006). However, direct U-series dating of the mekosuchine tooth from unit 6A yielded an age exceeding 450000 years (Grün *et al.* 2010), indicating that some elements within the deposit may have been reworked and that the specimen is probably pre-human and not late Pleistocene in age.

There are many fossils that have an ambiguous Pleistocene temporal provenance, and it is possible that some of them actually date to the late Pleistocene or Holocene. More precise dates for such fossils would be useful in providing additional taxonomic and palaeobiogeographical context to the puzzle of crocodylian diversity and evolution not only during the last 129000 years, but even more broadly in the Cenozoic. Conversely, some material previously assumed to be from the late Pleistocene may, in fact, be significantly older. Age uncertainties also affect material outside of mainland Australia. One noteworthy example is the enigmatic crocodylian '*Gavialis papuensis*' De Vis, 1905 from Busai, Muya (also referred to as Woodlark Island) in the Solomon Sea (Molnar 1982b). '*Gavialis papuensis*' is one of the least understood crocodylians from Australasia, both morphologically and taxonomically, due to the highly fragmented condition of its remains (for a recent review, see: Ristevski *et al.* 2023a). Its age is also uncertain but presumed to be Pleistocene (Molnar 1982b, Willis 1987). What is accepted though is that '*Gavialis papuensis*' is a member of Gavialoidea Hay, 1930, a group of crocodylians that today is survived by two species that inhabit south and south-east Asia. Gavialoids inhabited Australia earlier in the Cenozoic and are now extinct, these being *Harpacochampsa camfieldensis* Megirian *et al.*, 1991 from the middle Miocene of the Northern Territory and *Gunggamarandu maunala* Ristevski *et al.*, 2021 from the Pliocene or Pleistocene of south-eastern Queensland. '*Gavialis papuensis*' is, therefore, a third, and potentially the geologically youngest, gavialoid known from Australasia. Whether it dates to the late Pleistocene or older is currently unknown, but if '*Gavialis papuensis*' is demonstrated to be a late Quaternary taxon, it would indicate that gavialoids persisted in the region until relatively recently.

With the current lack of robust dates for much of the crocodylian material from Australasia, there are many outstanding questions particularly related to the extinction timing of mekosuchines. Some of the mainland Australian mekosuchine material discussed above may eventually be proven to be older than late Pleistocene and should for the time be treated as tentatively late Pleistocene in age until it is properly dated. It is, therefore, strongly recommended that future studies, where and when possible, attempt to obtain reliable dates for Quaternary crocodylian specimens.

CONCLUSION

The late Quaternary crocodylian fossil and zooarchaeological record from Australasia is characterized by fragmentary material thus far recognized from 19 Holocene-aged archaeological sites located throughout the region and seven late Pleistocene palaeontological sites primarily concentrated on mainland Australia and few in the south-west Pacific. The archaeological record of mekosuchines in Australasia is currently known only from New Caledonia, Vanuatu, and Fiji, whereas the Sahulian mekosuchines are thus far represented only in the palaeontological record. The Holocene archaeological record of Australia, Torres Strait, and New Guinea contains highly fragmentary remains of *Crocodylus*. All the currently known archaeological material comes from coastal or near-coastal sites and is most likely referable to *C. porosus* or, in the case of some mainland Australian remains, potentially *C. johnstoni*, although their fragmentary conditions preclude definitive specific identification in most cases. All but one of the Holocene archaeological sites that have yielded crocodylian material from Australia, Torres Strait, and New Guinea match the historic post-European colonial and present-day ranges inhabited by *C. porosus*, *C. johnstoni*, and/or the New Guinean *Crocodylus* species. *Crocodylus johnstoni* is the only extant crocodylian that has a substantial palaeontological record thanks to a fossil dentary referable to this species. In contrast to *C. johnstoni*, the fossil record of *C. porosus* is tentative because of the much more fragmentary nature of the known material that may be confidently attributable to this species. There are no recognizable remains either from the palaeontological or archaeological records that can be assigned to the *Crocodylus* species endemic to New Guinea. Crocodylian representation in rock art is known since the late Pleistocene, with these being interpreted by archaeologists as stylized depictions of *C. johnstoni* and *C. porosus*. The distribution of crocodylian rock art corresponds with the modern ranges of extant *Crocodylus* populations in Australia and New Guinea.

The Holocene archaeological record from Australia, New Guinea, and nearby islands has produced remains of *Crocodylus* spp. that appear to have been used by humans as a food source and at least in one case as a pendant. However, crocodylian remains are overall relatively rare at archaeological sites and, when present, are typically represented by only a few fragmented bones. This scarcity suggests that humans did not frequently hunt crocodiles compared to other fauna. One possible reason for this is that non-juvenile individuals of species like *C. porosus* are large and potentially lethal to humans, making them dangerous and difficult to hunt or capture. These factors would have made engagement with *C. porosus* and other *Crocodylus* species hazardous, which probably deterred frequent human interaction or predation. In contrast, the relatively small-bodied mekosuchines from the south-west Pacific may have been perceived as less threatening by humans, which could have made them more accessible targets for hunting and potentially more often used as a food resource.

At present, there are two major impediments to a more thorough understanding of crocodylian diversity and extinction in Australasia—the relative scarcity of fossil and sub-fossil specimens and the lack of reliable dates for most of the material. The lack of robust ages for most fossil specimens leaves uncertainties regarding the last known occurrences of mekosuchines. Some Pleistocene-aged sites across Australasia, predominantly in Australia and including Muyua in the Solomon Sea, have yielded crocodylian remains whose exact temporal placement within the past 2.5 million years remains unresolved. Likewise, some material that has been considered as late Pleistocene in age should be re-evaluated in the future by subjecting it to direct dating in order to constrain its precise age. Without more reliable dating it is unclear which, if any, additional specimens can be confidently assigned to the late Pleistocene.

The reason(s) for the extinction of mekosuchines on mainland Australia, whether climatic, environmental, anthropogenic, or a combination of some or all of these factors, is unclear. To date, there are no known mekosuchine remains found in archaeological sites and no known representation in rock art that would confirm any kind of interaction between humans and living mekosuchines anywhere in Sahul. That, coupled with the highly fragmentary nature and uncertain ages of the majority of Pleistocene mekosuchine fossils from Australia further confounds elucidation of the cause for their demise. Nevertheless, it appears that mekosuchine extinction in Australia coincides with the broader disappearance of some megafauna in Sahul, with a potentially long period of co-existence with humans. The last known mekosuchines survived on New Caledonia, Vanuatu, and Fiji until the Holocene but went extinct within a few centuries after humans settled those islands. Some mekosuchine remains from the south-west Pacific were discovered in association with human artefacts and/or middens, suggestive of interaction between humans and these unique crocodylians. In one instance, there is evidence of rat gnawing marks on a crocodylian limb bone from Vanuatu, suggesting that the Vanuatuan crocodylian was impacted by invasive species introduced by humans. Although definitive proof linking humans to the extinction of these insular mekosuchines is limited, direct or indirect human involvement appears to be the most likely cause for the disappearance of the last mekosuchine crocodylians.

The ongoing extinctions and high extinction rates of the Anthropocene, particularly marked in Australia in spite of research and conservation efforts (Woinarski *et al.* 2015a, b, Legge *et al.* 2023), demand novel interdisciplinary efforts and new applications of archaeological and palaeontological research. Our study highlights the value of linking research efforts by palaeontologists and archaeologists to understand extinctions, shifts in biodiversity, and the stability and resilience of ecosystem services today. Crocodylians represent a key taxonomic group of predators whose changing diversity and ecosystem function hold critical clues to understanding both long-term and recent anthropogenic impacts, as well as their legacies, and to implement effective landscape management today. Further research of the Australasian crocodylian record, including chronometric dating, analysis of ancient proteins and DNA, and stable isotope studies of fossils, would greatly help to clarify extinction timelines, biology, and environments. Systematic rock art studies to examine cultural perceptions and uses, as well as distribution patterns, are greatly warranted as well, as is the targeted recovery of further fossil and archaeological material. Such research would benefit greatly from engagement with Indigenous land managers and Indigenous Knowledges to build new frameworks for understanding and protecting some of the world's key remaining apex predators in the Anthropocene.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The data underlying this article are available in the article.

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